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9Schmidt et al: Weather-driven variation in cycles

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11**Weather-driven change in primary productivity explains variation in the amplitude of two**

12**herbivore population cycles in a boreal system**

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24

25Abstract

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2Author Contributions: EAR designed the vole study and EAR and MJF collected the vole data. CLM designed the
3hare project and collected the hare data. JHS analyzed the data and wrote the manuscript. All authors contributed
4to the conceptual integration of the datasets, discussed the results, and made substantive comments on the
5manuscript.

26Vertebrate populations throughout the circumpolar north often exhibit cyclic dynamics, and
27predation is generally considered to be a primary driver of these cycles in a variety of herbivore
28species. However, weather and climate play a role in entraining cycles over broad landscapes
29and may alter cyclic dynamics, although the mechanism by which these processes operate is
30uncertain. Experimental and observational work has suggested that weather influences primary
31productivity over multi-year time periods, suggesting a pathway through which weather and
32climate may influence cyclic herbivore dynamics. Using long-term monitoring data, we
33investigated the relationships among multi-year weather conditions, measures of primary
34productivity, and the abundance of two cyclic herbivore species: snowshoe hare and northern
35red-backed vole. We found that precipitation (rain and snow) and growing season temperatures
36were strongly associated with variation in primary productivity over multi-year time horizons. In
37turn, 4-fold variation in the amplitude of both the hare and vole cycles observed in our study area
38corresponded to long-term changes in primary productivity. The congruence of our results for
39these two species suggests a general mechanism by which weather and climate might influence
40cyclic herbivore population dynamics. Our findings also suggested that the association between
41climate warming and the disappearance of cycles might be initiated by changes in primary
42productivity. This work provides an explanation for observed influences of weather and climate
43on primary productivity and population cycles and will help our collective understanding of how
44future climate warming may influence these ecological phenomena in the future.

45**Keywords** Alaska, bottom-up, Denali National Park, growing degree days, population dynamics,
46precipitation, primary productivity, red-backed vole, snowshoe hare

47**Introduction**

Extensive effort has been directed towards understanding the mechanisms responsible for initiating and driving the cyclic population dynamics of vertebrates in the circumpolar north (Keith et al. 1984, Boonstra et al. 1998, Krebs et al. 1995, 2001a, Krebs 2011, 2013). In North America, predation is thought to be the dominant force driving the 10yr snowshoe hare [*Lepus americanus*] cycle observed across Canada and Alaska (Krebs et al. 2001a,b, 2013, 2014b, Krebs 2011), although some form of food limitation has also been implicated (Keith and Windberg 1978, Bryant 1981, Bryant et al. 1985, Krebs et al. 1995, 2014b, Hodges et al. 2001). Many species of microtine rodents also exhibit cycles at northern latitudes (Stenseth et al. 1999, Krebs 2013), however these cycles generally occur every 3-5yrs and are less commonly observed in North America (Boonstra and Krebs 2012, Krebs 2013). Populations of microtine rodents are also regulated in part by finite food resources (Boonstra et al. 2001, Huitu et al. 2003, 2007, Krebs et al. 2010, Johnson et al. 2017) and grazing-induced changes in food plants (Seldal et al. 1994, Reynolds et al. 2012, Wieczorek et al. 2014), though food limitation alone may be insufficient to cause the observed cycles (Krebs et al. 1995, Hodges et al. 2001, Krebs et al. 2001b, Krebs 2013, Prevedello et al. 2013). Similar to the case of snowshoe hares, top-down control through predation is generally thought to play a dominant role in microtine cycles (Hanski et al. 1993, Korpimaki and Krebs 1996, Korpimaki et al. 2002, 2004, Therrien et al. 2014, Fauteux et al. 2015b, Ginzburg and Krebs 2015).

In addition to the effects of food resources and predation, weather and climate patterns are implicated in cyclic dynamics. Seasonality and severe winter conditions may be necessary for the existence of cycles in general (Hansen et al. 1999, Yoccoz and Ims 1999, Stenseth et al. 2003, Bierman et al. 2006), and microtine rodents in particular are reliant on the insulative properties of snow for survival during extended winter periods (Reid and Krebs 1996, Korslund

71and Steen 2006, Bilodeau et al. 2013, Terraube *et al.* 2015). Additionally, climate processes
72influence cycle synchronicity across broad landscapes (Stenseth et al 1999, 2002, Krebs et al.
732001b, 2002, 2013 Kausrud et al. 2008, Hone et al. 2011, Yan et al. 2013), and recent changes in
74climate have been linked to the collapse of cycles in some areas (Hornfeldt 2004, Hornfeldt et al.
752005, Ims and Fuglei 2005, Ims et al. 2008, Cornulier et al. 2013). There is also some evidence
76that the impacts of weather and climate conditions on cycles may accrue over multiple years,
77possibly through changes in predator efficiency (Yan et al. 2013), however, the mechanisms by
78which weather and climate influence cycles remain uncertain. One possible mechanistic
79pathway is through weather or climate induced changes in vegetation quantity and/or quality, and
80hence forage for herbivores.

81 The role of weather conditions in altering primary production has received comparatively
82little attention in the population cycles literature, although research in other areas suggests a
83strong link. Experimental work in high latitude systems has shown that early snow-melt and
84warmer and wetter conditions during the growing season result in increased plant productivity
85through time, in part through increased soil nutrient turnover (Wipf and Rixen 2010, Natali et al.
862012, Schaeffer et al. 2013, Sistla et al. 2013). The role of multi-annual weather patterns on
87plant productivity in the boreal forest has also been demonstrated empirically through long-term
88observational studies (Krebs et al. 2009, Roland et al. 2014, Nicklen et al. 2016). While annual
89variation in primary productivity might not be expected to induce cycles, climate-driven changes
90in primary production may provide a mechanistic explanation for lagged relationships between
91population cycles and climate (e.g., Yan et al. 2013). There has been some exploration of the
92direct effects of weather on cycle amplitude (e.g., Krebs et al. 2014a), but we are not aware of a

93direct assessment of multi-annual changes in weather and climate as drivers of variation in
94herbivore population cycles through the influence on primary productivity.

95 We used long-term monitoring data to investigate the effects of weather-induced
96variation in primary productivity on the cyclic dynamics of 2 herbivore species occurring in
97Denali National Park and Preserve (hereafter Denali): northern red-backed voles [*Myodes*
98*rutilus*], and snowshoe hares (hereafter voles and hares, respectively). We hypothesized that
99multi-year weather conditions may drive variation in primary productivity, in turn, influencing
100the vole and hare cycles observed in our study area. Our primary objectives were to: 1) assess
101the relationship between multi-year weather conditions and corresponding indices of primary
102productivity, and 2) assess the relationship between measures of primary productivity and
103variation in cyclic dynamics in voles and hares. If a sequential link between weather, primary
104productivity, and herbivore cycles were established, it would provide a common mechanism by
105which climate factors could drive variation in 2 cyclic herbivore populations in North America.

106**Materials and methods**

107*Study area*

108Our study area encompassed 2522 km² in the northern foothills of the Alaska Range within
109Denali in interior Alaska, USA (see McIntyre and Schmidt 2012; Fig. 1). The study area
110encompassed boreal-montane ecosystems including conifer and mixed conifer and deciduous
111forests in the lowlands ranging upwards into subalpine shrublands then through an alpine tundra
112zone into barren rock and ice in the highest elevations (Roland et al. 2013). The topography
113ranged from rugged mountainous terrain to broad glacial valleys and floodplains, as well as
114rolling upland areas. Elevations ranged from ~400m-1400m. The area experienced long, cold,
115dry winters and short, warm summers. Historically, the average annual temperature was -3°C,

with an average high of 20°C and an average low of -22°C (Shulski and Wendler 2007). Average annual precipitation was 38.1cm (Shulski and Wendler 2007). Annual snowfall averaged 206cm, which is usually concentrated in the months of November and December (Sousanes 2008).

Field Methods

We summarized weather data from the climate station located at Denali headquarters within our study area (Fig. 1). We used temperature records to calculate the number of growing degree days (GDD; base temperature 5° C) accumulated between April-August for each year of our study. We also obtained the total recorded precipitation for the same period (PPT) and calculated the average snow depth over the previous winter (Oct 15-April 1) as an index of winter snow conditions (SNOW). We selected these measures because they broadly represent weather factors associated with major sources of variation in plant productivity and nutrient turnover (e.g., Wipf and Rixen 2010, Natali et al. 2012, Schaeffer et al. 2013, Sistla et al. 2013, Roland *et al.* 2014). We also developed a binary early winter severity index to represent potentially thermally stressful conditions for voles that could cause increased early winter mortality (i.e., Reid and Krebs 1996), possibly lowering their abundance in the subsequent year. The early winter severity index (freeze) was a binary variable indicating years with >5 days in early winter (October-December) with snow depths <15 cm and daily minimum temperatures <-17.8°C. To provide an annual measure of primary productivity, we calculated the average annual maximum Normalized Difference Vegetation Index (NDVI), based on satellite imagery (AVHRR; 1km² pixels), across the study area from 1990-2013 (values were not available prior to 1990). Due to the small size of the vole study site relative to the spatial grain of the satellite imagery, we used measures of NDVI based on the larger snowshoe hare study area for the vole

139analysis. We assumed that measures of NDVI over this larger scale would reflect conditions at
140the local scale of the vole study site and expected that the results based on measures of NDVI at
141a larger scale would be more conservative (i.e., less likely to detect an effect) due to local scale
142variation in productivity that would be averaged over the larger area. These weather and primary
143productivity variables were then used as covariates for analysis.

144 We sampled the vole population on 4 plots at a site in Denali centered on (63° 43' 47" N,
145longitude 148° 58' 52" W) during August from 1992-2014 (Fig. 1). Each plot consisted of a 10 x
14610 grid of Sherman live traps spaced 10 m apart over 0.81 ha. Two plots were located along the
147Rock Creek riparian zone (riparian plots) and 2 were located approximately 500 m away on a
148forested ridge (forest plots). One forest plot and one riparian plot were sampled annually, a
149second forest plot was sampled 1997-2014 (except 2004), and a second riparian plot was
150sampled during 1992-1993 and 1997-2014. Each trap contained bedding material and was baited
151with sterilized sunflower seeds. Trapping sessions were 4-5 days long with 3 trap checks per
152day, resulting in 10-15 sampling occasions per plot per year. Captured individuals were
153identified to species, scanned with a passive integrated transponder (PIT) tag reader to identify
154previously captured individuals, injected with a uniquely identifiable PIT tag if unmarked, and
155then released. The final dataset consisted of 2277 capture histories over the 23 year period.

156 We indexed annual hare abundance from 1988-2014 as the average number of adults
157observed per day during routine fieldwork from mid-April to late June as part of a larger project
158(see McIntyre and Adams 1999, McIntyre and Schmidt 2012). All observations were made and
159recorded by the same individual (C. McIntyre) using a standardized approach for the entire
160period (McIntyre and Schmidt 2012). While the annual indices could not be converted to true
161abundance, we were confident that this measure accurately represented relative abundance

162between years and the frequency and relative amplitude of the hare cycle in Denali (McIntyre
163and Schmidt 2012, Krebs et al. 2013). Our hare index was in general agreement with an
164assessment of the hare cycle in nearby areas (Arthur and Prugh 2010, Krebs et al. 2013), further
165supporting our assertion that our data accurately represented the relative abundance and phase of
166the hare cycle in Denali.

167*Statistical Analysis*

168Primary productivity

169Measures of NDVI provide a meaningful annual index of primary productivity at large scales
170(Kerr and Ostrovsky 2003), however, we wanted to explore the relationship between weather
171conditions and changes in primary productivity over multi-year windows. We hypothesized that
172primary productivity may be a function of weather patterns that influenced growing conditions
173over time (e.g., Wipf and Rixen 2010, Natali et al. 2012, Schaeffer et al. 2013, Sistla et al. 2013),
174presuming plant growth may increase when the weather is warmer, wetter, and less snowy.
175Therefore, we fit a series of models to running averages of NDVI over the previous 1-5 years
176using corresponding running averages of GDD, PPT, and SNOW as covariates. All variables
177were standardized to have a mean = 0 and SD = 1 to improve convergence and allow direct
178comparisons of effect sizes among covariates. The general model can be written as:

$$179NDVI_i = \beta_1 GDD_i + \beta_2 PPT_i + \beta_3 SNOW_i$$

180where i represents the running average i in 1...5 years. We used the adjusted R^2 value as a
181measure of model fit and selected the most appropriate value of i based on the vole and hare
182analyses (see below).

183Voles

184 To estimate vole abundance and density, we used spatially-explicit capture-recapture models
185 (Royle and Dorazio 2008, Efford et al. 2009, Borchers 2012, Efford and Fewster 2013) fit in a
186 Bayesian hierarchical framework (e.g., Royle and Young 2008, Gardner et al. 2009, 2010, Royle
187 et al. 2009). Spatially-explicit capture-recapture approaches utilize the locations of recaptures to
188 estimate the activity center of each individual, while also addressing the decline in detection
189 probability with distance of the activity center from each trap (Royle and Young 2008, Gardner
190 et al. 2009, Efford and Fewster 2013). This straightforward combination of the process and
191 detection models allows the direct estimation of abundance or density within the sampling area
192 without requiring the concept of the somewhat ambiguous effective trapping area (Efford and
193 Fewster 2013). Data augmentation (Royle et al. 2007) was employed to address the problem of
194 an unknown number of activity centers within the sample area (Gardner et al. 2010).

195 We used the spatial mark-recapture model presented by Gardner et al. (2009) to estimate
196 the number of individuals, N , with activity centers within the sampling area, S . Density was
197 defined as N/S . We investigated the importance of multiple covariates by formulating a model
198 for the inclusion probability, ψ_i . This is the probability that an individual from the augmented
199 data list is a member of the population (Gardner et al. 2009). This allowed us to assess the
200 influence of covariates on population size. We allowed capture probability to vary by year, and
201 included an individual random effect to account for heterogeneity in capture probability among
202 individuals in addition to variation due to the locations of each activity center. We included a
203 plot by year random effect in the model for ψ_i to account for differences between plots and
204 years that were not explained by the covariates.

205 Prior to conducting the Bayesian analysis, we used an exploratory analysis of the raw
206 capture data to identify potentially useful covariates. We used this approach due to the

prohibitively long run times that would be required for model selection in a Bayesian framework. We fit generalized linear models to the average number of unique captures in each year to (i.e., raw data) using sine and cosine terms with 2, 3, or 4 year periodicity to address cyclic patterns in abundance. This range of values was selected after an inspection of the auto-correlation function. Although we could have used other time series approaches to address cycle periodicity (e.g., threshold autoregressive modeling; Stenseth et al. 1998), we chose to employ a fixed cyclic pattern for simplicity and because our primary questions were related to variation in cycle amplitude. Our approach to modeling the basic cyclic pattern was expected to have no impact on our assessment of the factors affecting cycle amplitude. After using AIC to select the best model describing the basic cycle, we explored the potential relationship between vole abundance and the early winter severity index (freeze) and the range of running averages (i.e., 1 to 5 years) for NDVI for our study area. Based on this exploratory analysis, we selected NDVI₅ as the most informative predictor of variation in vole abundance for final model fitting (see results). We then fit the model to the data in a Bayesian framework to assess whether the apparent relationships from the exploratory step held under formal analysis. The most general model for the probability of a potential individual being included in the population, ψ , can be written as:

$$\text{logit}(\psi) = \int + \beta_1 \sin\left(\left(\frac{2\pi}{L}\right) * t_i\right) + \beta_2 \cos\left(\left(\frac{2\pi}{L}\right) * t_i\right) + \beta_3 \text{NDVI}_5 + \beta_4 \text{freeze} + e_{ij}$$

where int is the intercept, the β_k are parameters, L is the cycle period length (i.e., 2, 3, or 4 years), t_i is the annual time step (years 1-23), and e_{ij} is a random effect adjustment term for each year, i , and site, j . For the 1992-1994 period, when NDVI₅ values were not available, we used the longest running average possible (i.e., 2, 3, and 4 years respectively). Post-hoc analysis using only data from 1995-2014 produced nearly identical results, suggesting the use of slightly shorter NDVI averages for the first 3 years of our series did not materially affect our results. Therefore,

we only present results based on the full 1992-2014 dataset. Models were fit using program R (v. 2.14.2, R Development Core Team 2012) and OpenBUGS (Thomas et al. 2006).

Hares

We log-transformed the annual hare index and used linear models to describe the cycle and select among covariates. We first inspected the autocorrelation function based on the time series data to assess the period length of the cycle. Based on these findings, we then fit models containing sine and cosine terms with a 9, 10, or 11 year period to assess whether cyclic terms were supported and to identify the appropriate period length. After selecting the best approximating model describing the basic cycle, we considered the covariates GDD_i , PPT_i , and $SNOW_i$ as proxies for $NDVI_i$. We used the weather data in this case because the hare dataset began 7 years prior to the availability of $NDVI$ for our study area. Our objective was to assess whether these proxies for $NDVI$ would predict variation in hare numbers. We did not consider the winter severity term as we did not expect hares to be as dependent as voles on snow cover for thermal protection during early winter. The most general model describing each index of abundance, *index*, can be written as:

$$\log(index) = \int + \beta_1 \sin\left(\left(\frac{2\pi}{L}\right) * t_j\right) + \beta_2 \cos\left(\left(\frac{2\pi}{L}\right) * t_j\right) + \beta_3 GDD_i + \beta_4 PPT_i + \beta_5 SNOW_i \text{ where } int \text{ is}$$

the intercept, β_k are parameters, L is the period length (9, 10, or 11 years), and t_j is the annual time step (i.e., 1-27 years). We first used AIC to select the appropriate terms describing the cycle (i.e., sine and cosine terms) and period length. We then used AIC to identify whether the weather covariates improved model fit. We also conducted a post-hoc exploratory analysis using only the 1995-2014 data, replacing the three weather covariates with $NDVI_i$, to confirm that any relationships were consistent and increase our confidence in the results.

Results

253 *Primary productivity*

254 NDVI_t was highest in multi-year periods that were warmer, wetter, and less snowy,
 255 corresponding to conditions in the mid-2000's (Fig. 2). Model fit improved as the length of the
 256 moving average increased, and the 3 weather variables (GDD₅, PPT₅, SNOW₅) explained nearly
 257 all of the variation in NDVI₅ between 1995 and 2014 ($R^2 = 0.94$; Fig. 2). This result indicated a
 258 direct link between average weather conditions over the previous 5 years and average NDVI over
 259 the same time period. We present the results for NDVI₅ because this variable was the best
 260 predictor for variation in vole cycle amplitude.

261 *Voles*

262 The average annual number of unique captures per plot varied from 6 to 81. We found strong
 263 support for the inclusion of both sine and cosine terms with period length = 3, indicating the vole
 264 population in our study area cycled regularly every 3 years (Table 1, Figs. 3, 4B). As predicted,
 265 in years following those with severe early winter conditions, abundance was reduced, suggesting
 266 a reduction in survival in early winter in those years (Table 1, Fig. 4B). Model selection results
 267 indicated that the model containing NDVI₅ fit better than versions containing NDVI₄ ($\Delta AIC =$
 268 2.6) or NDVI₃ ($\Delta AIC = 4.7$), and there was little support for NDVI averaged over shorter time
 269 periods (i.e., $\Delta AIC > 15$). The best approximating model indicated that cycle amplitude varied 4
 270 fold in direct relation to NDVI₅ (Fig. 4). Estimated densities based on the Bayesian model
 271 ranged from 2.2/ha during the 1994 low to 36.6/ha during the 2008 peak. The strong relationship
 272 between NDVI₅ and vole cycle amplitude suggests that variation in vole densities was directly
 273 related to primary productivity throughout the 3 yr cycle. The period length of the cycle
 274 remained consistent through time despite variation in both winter severity and primary
 275 productivity.

276Hares

277Our index of hare abundance ranged from 0.3 to 40.6 during our 27yr study. The hare cycle was
278best represented by sine and cosine terms with a period length of 10 (Table 2, Fig. 3). Models
279containing 4 and 5 year running averages of the 3 weather variables received equal support and
280outperformed averages over shorter intervals. For consistency with the vole results, we present
281estimates from the model containing 5 year running averages of GDD₅, PPT₅, SNOW₅.
282Although the period of the hare cycle (10 years) was longer than that of voles (3 years), the
283population-level response to these predictors of primary productivity was similar (Fig. 4C).
284Although NDVI₅ values did not exist for the early years of the hare dataset, the model containing
285weather conditions identified as the primary drivers of NDVI₅ predicted variation in the
286amplitude of the hare cycle well ($R^2=0.82$). An exploratory analysis using a subset of the data
287for the period when NDVI₅ was available produced very similar results, supporting these
288conclusions (results not shown). There was little support for a model lacking the weather
289variables ($\Delta AIC = 20.7$) and the fit of the reduced (i.e., cyclic terms only) model was lower
290(adjusted $R^2=0.44$), indicating strong support for a link between long-term weather and hare
291abundance. The third hare peak was 4 fold higher than the previous two and was synchronous
292with a peak in vole densities of similar magnitude (Fig. 4). Both peaks also corresponded with
293the period of highest NDVI₅. Thus, although hares and voles cycled at much different rates and
294exhibit different life history characteristics, they shared a contemporaneous relationship with
295primary productivity.

296Discussion

297Our results demonstrate that multi-year weather patterns were directly related to variation in
298measures of primary productivity at the landscape-scale in our boreal study system, which were

299in turn positively related to the dynamics of two widely distributed cyclic herbivore species,
300hares and voles. These findings establish sequential relationships between long-term weather
301patterns, primary productivity, and cyclic dynamics, thereby increasing our collective
302understanding of the processes underlying these important phenomena. Weather and climate
303patterns have been identified as important factors in the dynamics of many cyclic species, but the
304mechanism through which they influence these populations had heretofore been elusive
305(Stenseth et al. 1999, Watson et al. 2000, Cattadori et al. 2005, Kausrud et al. 2008, Hone et al.
3062011, Yan et al. 2013). The establishment of these linkages provides a potential mechanistic
307explanation for the observed diminution of some cycles (Hornfeldt 2004, Hornfeldt et al. 2005,
308Ims and Fuglei 2005, Ims et al. 2008, Cornulier et al. 2013) through climate-induced changes in
309primary productivity.

310*Weather and primary production*

311Our results suggest that primary productivity in Denali varies at the landscape-scale in response
312to annual precipitation (both rain and snow) and summer temperatures, and that these responses
313operate over multi-year time spans. That is, annual time-steps may not always be the appropriate
314temporal window for considering the relationships among weather variables and primary
315productivity in this region. The positive influence of warmer, wetter, and less snowy conditions
316we found were not surprising given other studies that have demonstrated similar links between
317annual metrics of broad-scale productivity (as measured by NDVI) and annual climate in high
318latitude regions (e.g. Goetz et al. 2005, Verbyla 2008, Berner et al. 2013). Specifically, shrub
319tundra areas (that occur over a large portion of our study area) showed increasing NDVI trends in
320response to increasing summer warmth (Verbyla 2008, Berner et al. 2013), some interior lowland
321boreal forest areas showed decreasing NDVI trends at least in part in response to drought (Goetz

et al. 2005, Beck et al. 2011), and delayed green-up has been related to deep snows in spring (Pettorelli et al. 2005, Wipf and Rixen 2010).

Although the specific climate-productivity relationships we found in Denali are not necessarily surprising, it is noteworthy that our data suggest that some weather-vegetation interactions governing NDVI accrue over multi-year windows. Possible explanations for the strong association between multi-year weather conditions and NDVI include a variety of processes including increased rates of nutrient turnover in response to warm and/or wet periods (e.g. Hobbie 1996, Natali et al. 2012, Schaeffer et al. 2013, Sistla et al. 2013) that may stimulate increased plant growth over multiple years, and the possibility that the deepening of active layer depths over a series of years may induce productivity effects that manifest over multi-year time scales (e.g. Beck et al. 2015). For example, tree ring studies in interior Alaska (including Denali) routinely showed significant responses to previous years' weather (Lloyd et al. 2013, Walker and Johnstone 2014, Girardin et al. 2016, Nicklen et al. 2016). Further, a recent investigation into white spruce reproduction in Alaska revealed significant weather effects on seed production over a four-year period (Roland et al. 2014). Additionally, the impacts of extreme weather events showed delayed responses that may occur even two years later (Zona et al. 2014). Such relationships will not be apparent when using strictly annual metrics without utilizing lagged effects due to high interannual variability and the unquantified influence from previous annual time steps. While our current data cannot confirm the mechanisms behind the conspicuous association, a fertile area for future work may be the role of multi-year weather patterns in regulating long term trends in primary productivity.

Hare and vole cycles

344Extended winter periods, such as those experienced in Denali, are often considered necessary for
345the existence of population cycles at high latitudes (Hansson and Henttonen 1985, Yoccoz and
346Ims 1999, Aars and Ims 2002, Stenseth et al. 2003, Hornfeldt et al. 2005, Bierman et al. 2006).
347While it is unlikely that food resources are limiting for either hares or voles during the growing
348season, our results suggest that primary production might play a role in limiting populations
349during the subsequent winter months (e.g., Huitu et al. 2003, 2007). The link between weather
350and primary productivity also suggests a mechanism by which changes in season length and
351productivity may result in the dampening or elimination of population cycles in some areas in
352association with climate change (Ims et al. 2008, Cornulier et al. 2013, Korpela et al. 2013).
353Although we did not observe a dampening of cycles in Denali, we speculate that the diminution
354or elimination of cycles in other areas might occur through a reduction in the limiting effects of
355winter through increased food resources, or alternatively, a general amelioration of the winter
356period (i.e., length or severity) sufficient to avoid population limitation. However, the specific
357causal variables and the sign of the relationships will likely vary among ecosystems, climatic
358regions, and/or geographic locations, and we expect future work in other areas may reveal
359additional relationships between climate and primary production.

360 The 3 yr vole cycle we documented was unique for this species in North America
361(Boonstra and Krebs 2012, Boonstra et al. 2016), although the basic cyclic pattern was similar to
362that of populations in Fennoscandia and elsewhere in Eurasia (Stenseth et al. 1996, Stenseth
3631999). Existing studies in Alaska have provided limited information on long-term dynamics or
364evidence of cycles, although long-term datasets are uncommon (e.g., Whitney 1976, West 1982,
365Whitney and Feist 1984). We expect that cyclic dynamics may exist in other vole species (e.g.,
366Fauteux et al. 2015a), or in other portions of North America, however, an assessment of the scale

and breadth of such cycles is dependent on the implementation of additional monitoring programs and further analysis of any existing datasets. Our results are consistent with past findings that microtine rodent populations at high latitudes are generally dependent on snow cover to mitigate the effects of extreme cold (Reid and Krebs 1996, Boonstra and Krebs 2006, Korslund and Steen 2006, Bilodeau et al. 2013, Fauteux et al. 2015b). Interestingly, severe winter conditions influenced vole cycle amplitude but had no apparent effect on periodicity, suggesting winter severity itself does not cause cycles directly. Instead, the link between primary productivity and amplitude throughout the cycle suggests food might be implicated as a limiting factor (Boonstra et al. 2001, Huitu et al. 2003, 2007, Previtali et al. 2009, Krebs et al. 2010), presumably during the extended winter period when individuals are dependent on finite food resources.

A critical finding of our study was the discovery of an apparent relationship between long-term measures of primary productivity and abundance throughout both the 10yr hare and 3yr vole cycles. Although only 3 hare peaks were observed during our study period, the nearly identical pattern of increased amplitude in the vole cycle during the same time frame strengthens our conclusion that primary productivity may limit cycle amplitude in both species. The importance of large-scale weather patterns on hare cycles has previously been identified (Stenseth et al. 1999, Yan et al. 2013), although the causal link remained unclear. The direct relationship between weather and primary productivity establishes a potential mechanism through which weather and climate could influence population cycles. We argue that the most parsimonious explanation for the 4-fold variation in cycle amplitude is that multi-year levels of primary productivity placed an upper limit on both the hare and vole cycles. This is consistent with the theory of bottom-up control which has been demonstrated in similar species (Flowerdew

et al. 2017, Johnson et al. 2017). Our results suggest that variation in amplitude was driven by limited resources, with higher peak densities occurring during periods of high primary productivity when food resources are presumably more abundant. The congruency of our results, despite considerable differences in the spatial and temporal scales captured in each dataset, supports our conclusions.

There are two important mathematical properties that warrant further discussion in the context of interpreting our results. First, variation in cycle amplitude has an equal and opposite effect on opposing phases of the cycle (all else being equal), therefore, as amplitude increases, both the high and low phases become more extreme. This behavior resulted in a potentially counterintuitive finding that low-phase densities were lower when NDVI was higher. However, rather than being incongruent with our bottom-up hypothesis, these reduced low-phase densities were a direct consequence of increased cycle amplitude during periods of high NDVI. Second, population cycles differ from basic cyclic patterns (e.g., a sine wave) in that the low phase of population cycles is constrained to be ≥ 0 while the high phase has no upper bound. Due to this constraint, there is less potential for variation among low-phase densities as compared to peak densities. Together these explanations help clarify that our findings are consistent with our bottom-up hypothesis throughout both the hare and vole cycles, despite a few potentially unintuitive patterns.

Long-term, comprehensive monitoring programs (e.g., the Kluane project; Krebs et al. 2001a), are responsible for much of what we know about population cycles in the boreal forest. One of the primary strengths of long-term studies across taxa and trophic levels is the ability to consider cyclic dynamics in the context of the larger system. The largest contributions of our work to the overall understanding of population cycles in the north are: 1) the establishment of a

413direct link between weather conditions and primary productivity at the landscape-scale across
414multi-year time-steps, and 2) the potential role of weather-induced variation in primary
415productivity in controlling cycle amplitude in two disparate cyclic taxa. By extension, we
416hypothesize that the apparent role of primary productivity in limiting cycle amplitude in hares
417and voles suggests that bottom-up forces play a larger role in cycle dynamics than is currently
418thought (e.g., Krebs et al. 2013, 2014ab, Therrien et al. 2014, Ginzburg and Krebs 2015). We
419suspect the primary reason for our novel findings is that the multi-year nature of the links
420between weather, primary productivity, and cycle amplitude were heretofore unidentified. In
421light of our results, we suggest the reanalysis of existing datasets using indices of primary
422productivity over multiple years to investigate the extent to which our findings might be
423generalized to other systems. Such work should be relatively easy to conduct because NDVI
424data are widely available for the last 2 decades, and weather data generally exist over long time
425periods. Such work would directly assess the applicability of our findings to other areas and
426would expand our understanding of the role of primary productivity in population cycles in the
427north.

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Table 1. Parameter estimates from the Bayesian model (Eq. 2) describing variation in the density of voles in Denali National Park and Preserve, Alaska from 1992-2014.

Covariate	Mean	Lower 95%CrI	Upper 95% CrI
Intercept	0.26	0.06	0.41
Sine	-0.83	-1.10	-0.58
Cosine	-0.44	-0.73	-0.14
NDVI ₅	0.35	0.13	0.57
Early winter	-0.61	-1.01	-0.22
severity			

679

680

Table 2. Parameter estimates from the top model (Eq. 3) describing variation in the hare population index over time in Denali National Park and Preserve, Alaska from 1988-2014. The sine and cosine terms assume an 10 year periodicity, GDD_5 represents the 5 year running average of growing degree days April-August, PPT_5 represents the 5 year running average of precipitation April-August, and $SNOW_5$ represents the 5 year running average of average snow depth in the previous winters. Estimates are presented as means with standard errors in parentheses.

688

Covariate	Hares
Intercept	1.39 (0.12)
Sine	0.90 (0.13)
Cosine	0.18 (0.15)
GDD_5	0.56 (0.09)
PPT_5	0.32 (0.12)
$SNOW_5$	-0.50 (0.15)

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690

Figure 1. The location of Denali National Park and Preserve within the state of Alaska (inset), the general location of the vole survey plots, and the location of the climate station within our study area are shown. The dashed line indicates the area from which the average maximum NDVI values were calculated and the snowshoe hare index data were collected.

Figure 2. Plots of the five year running average of NDVI ($NDVI_5$; black), growing degree days (GDD_5 ; solid gray), summer precipitation (PPT_5 ; dashed gray), and average snow depth in the prior winter ($SNOW_5$; dotted gray) in Denali National Park and Preserve, Alaska from 1988-2014. Values have been scaled to have a mean = 0 and a SD = 1.

Figure 3. Autocorrelation function (ACF) plots for vole density from 1992-2012 (a) and the hare abundance index from 1988-2012 (b) in Denali National Park and Preserve, Alaska. Vertical lines in the ACF plots that extend above the horizontal dashed lines indicate statistically significant autocorrelations.

Figure 4. Plots showing the temporal relationship between $NDVI_5$ (a) and the northern red-backed vole (b) and snowshoe hare (c) cycles in Denali National Park and Preserve, Alaska from 1988-2014. Plots of observed (solid lines) and predicted (dashed lines) values are included as a visual assessment of model fit. Fine dotted lines on panel (b) indicate years with severe early winter conditions. Values have been scaled to have a mean = 0 and a SD = 1.

Fig. 1.

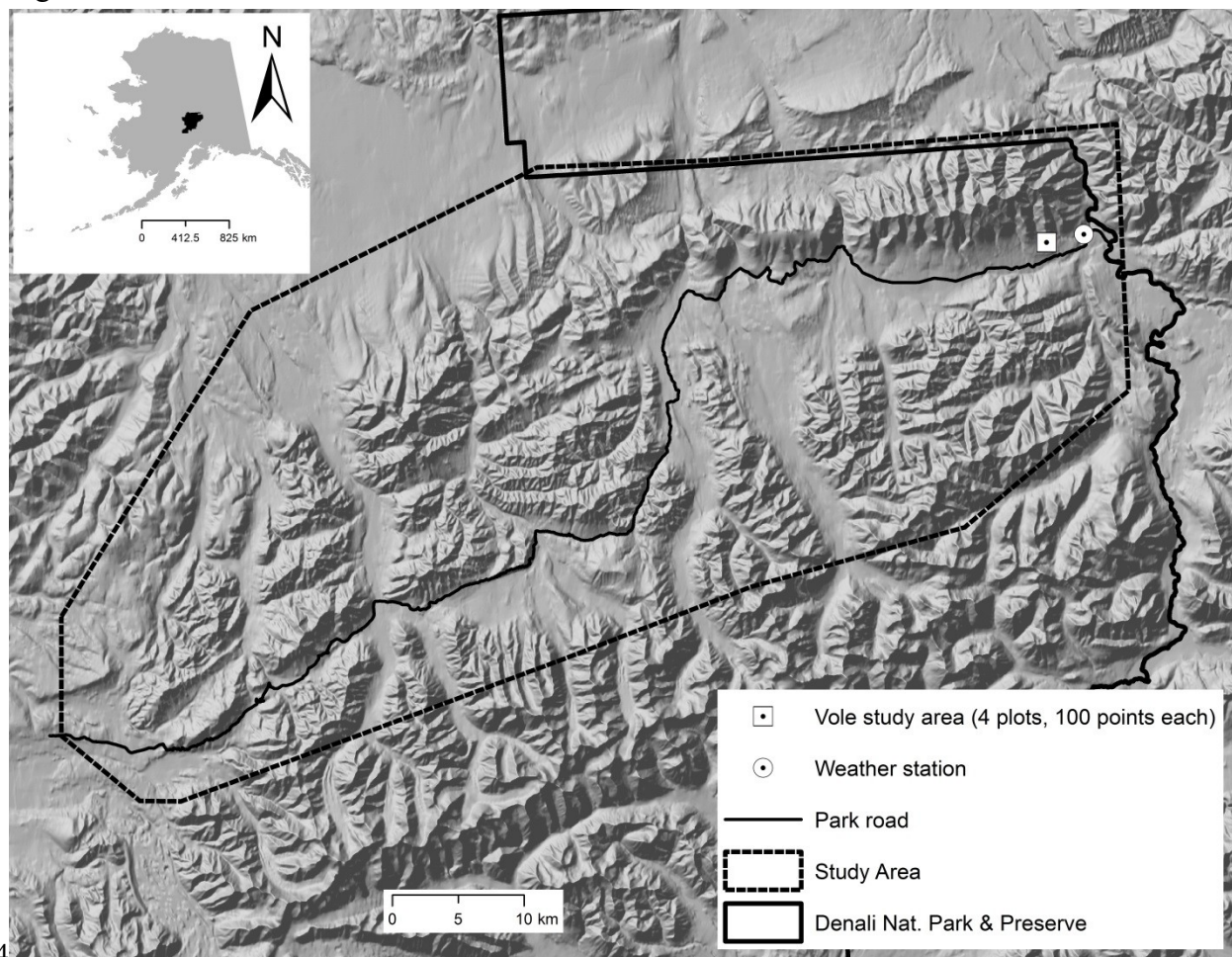


Fig. 2.

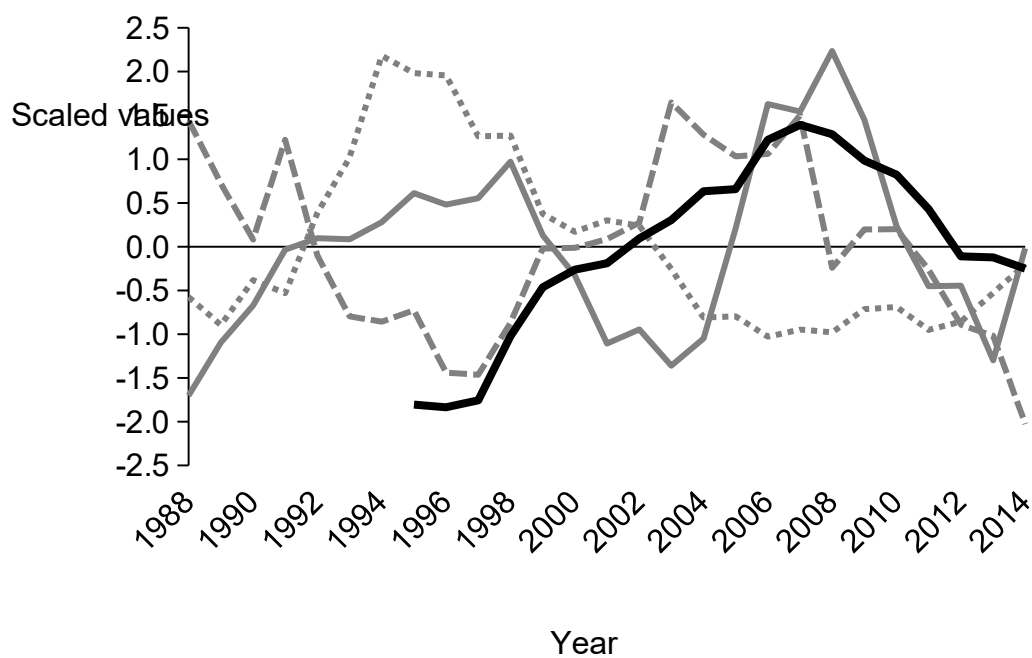


Fig. 3.

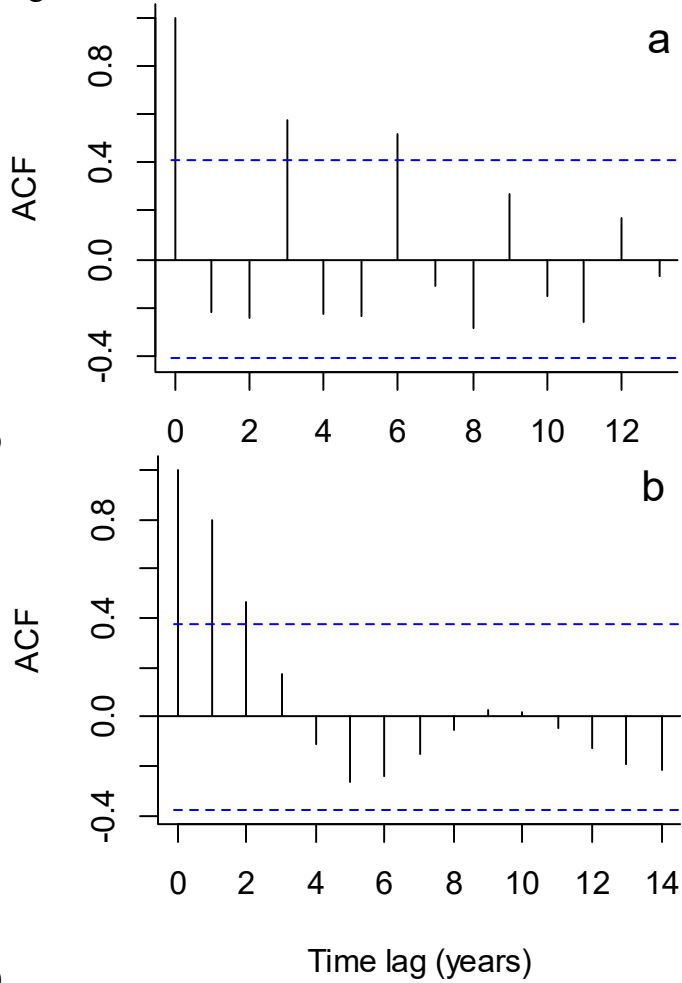


Fig. 4.

